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Molecular and morphological identification of *Phylloderma stenops* Peters, 1865 (Chiroptera, Phyllostomidae) and new records for Colombia

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Abstract

Based on revisionary work of recently collected material in Colombian museums we confirm the presence of *Phylloderma stenops* Peters, 1865 in 6 new localities for the country, including the first record of the species in the dry lowlands of the northern Caribbean coast, and the increase by more than 800 m of the elevational range of the species in Colombia. DNA-barcoding confirmed our morphological identification, and supported a paraphyletic composition of the cis-Andean populations. Our records exemplify the little knowledge on the ecogeographic distribution of this species and provide further evidence to consider this as a widespread but rare species.

Key words

DNA barcode, ecogeographic distribution, Pale-faced Bat.

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Introduction

The pale-faced Bat, *Phylloderma stenops* Peters, 1865, is the only representative of its genus and includes 3 recognized subspecies primarily based on morphometric and distribution data: *P. s. boliviensis* Barquez & Ojeda, 1979, from southeastern Bolivia, *P. s. septentrionalis* Goodwin, 1940, distributed in Central America, and the nominal subspecies *P. s. stenops* Peters, 1865, distributed throughout most of South America from the Guianas to southeastern Brazil (Goodwin 1940, Husson 1962, Handley 1966, Barquez and Ojeda 1979, Simmons and Voss 1998, Emmons and Feer 1999, Simmons 2005, Williams and Genoways 2008). *Phylloderma stenops* is considered a large and robust bat that externally may be confused with taxa of the genus *Phyllostomus* (Emmons and Feer 1999, Wetterer et al. 2000, Williams and Genoways 2008), an event that has facilitated its misidentification with species of the latter genus not only in the field but also in biological collections.

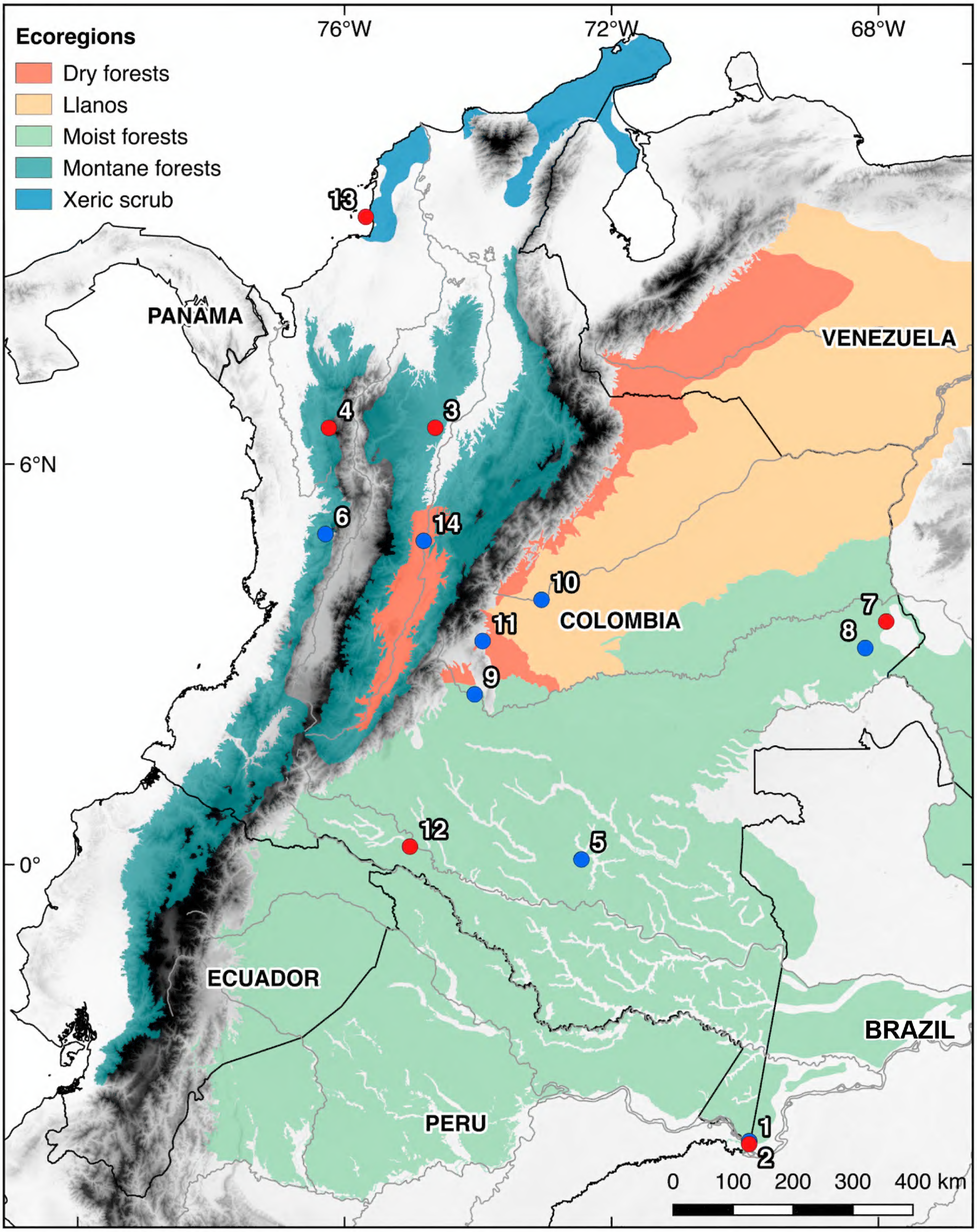

Figure 1. Collecting localities and ecoregions of *Phylloderma stenops* for Colombia. Red circles represent new records; blue circles correspond to previously published records (see text). Numbers correspond to localities in Table 2.

In Colombia, the species is known from a few records primarily from cis-Andean localities which are mostly categorized as terrestrial ecoregions (sensu Dinerstein et al. 2017) of moist forests (Fig. 1: localities 2, 5, 8 and 9) (Marinkelle and Cadena 1972, Lemke et al. 1982, Alberico 1994, Montenegro and Romero-Ruiz 1999), a single locality at the ecotone between montane and dry forests (Fig. 1: locality 11) (Sánchez-Palomino et al. 1993) and a single locality at the llanos (Fig. 1: locality 10). The only two available records with trans-Andean distributions come from northwestern Andean montane forests (Fig. 1: locality 6) (Alberico 1994) and some recent records at the Magdalena Valley dry forest (Fig. 1: locality 14) (Ramírez-Fráncel et al. 2015). All the available

records are distributed in an elevational range between 0 and 900 m a.s.l. Herein, we review the distribution of the genus in Colombia, providing new localities based on museum specimens as well as recently collected material, and we additionally corroborate our morphology-based identification using a DNA-barcoding approach.

Methods

In search for additional unpublished or misidentified records and to corroborate the identification of eight previously published records of the species (Sánchez-Palomino et al. 1993, Montenegro and Romero-Ruiz 1999, Ramírez-Fráncel et al. 2015) we visited the Colección Teriológica Universidad de Antioquia, Medellín (CTUA), Colección de Mamíferos "Alberto Cadena García", Instituto de Ciencias Naturales, Bogotá (ICN) and the mammal collection of the Museo de Ciencias Naturales de la Salle of the Instituto Tecnológico Metropolitano, Medellín (CSJ-m). For the morphology-based identification of all specimens, we followed the diagnostic characters described by Goodwin (1940, 1942), Husson (1962), Barquez and Ojeda (1979), and Williams and Genoways (2008).

To further corroborate the identification of the species we DNA-barcoded specimen CSJ-m 995—an adult individual that exhibits all the diagnostic characters of the species (see below)—and performed a phylogenetic analysis. Following a total DNA extraction using the UltraClean Tissue & Cells DNA Isolation Kit (MO BIO Laboratories, Inc.), part of the mitochondrial marker Cytochrome Oxidase Subunit I (COI) was PCR-amplified using the primer cocktail and thermal cycling conditions described in Ivanova et al. (2012). Amplicons were sequenced using amplification primers and dye-terminator chemistry on an ABI-3730xl automated sequencer. Sequences were edited and assembled in GENEIOUS® 9.1.8 (http://www.geneious.com, Kearse et al. 2012). The obtained sequence was deposited in GenBank with accession number MH298327. We downloaded all the available COI sequences of *Phylloderma stenops* from GenBank (Table 1) and to corroborate the genus-level identification we also downloaded sequences from at least one species of all the genera within the phyllostomid subfamily Phyllostominae (access numbers JF435806, JF447419, JF447421, JF447429, JF448940, JF449253, JF455242, JF455365, JF455386). All sequences were aligned with MUSCLE (Edgar 2004) and the resulting alignment was analyzed using maximum likelihood as implemented in GARLI 2.0 (Zwickl 2006), specifying 5 independent search replicates, and HKY+G+I as the best fitted nucleotide substitution model—based on the Bayesian Information Criterion implement in JMODELTEST

Table 1. Sequences of *Phylloderma* included in this report. * Correspond to unpublished data, ** corresponds to a sequence without voucher.

Genbank accession no.	Voucher	Country	COI (bp)	Source
EF080541	ROM111506	Guyana	608	Clare et al. 2007
EF080542	ROM98903	Guyana	657	Clare et al. 2007
EF080543	ROM106627	Guyana	657	Clare et al. 2007
EF080544	ROM107203	Guyana	657	Clare et al. 2007
EF080545	ROM104694	Guyana	657	Clare et al. 2007
EU096830	ROM117511	Suriname	657	Borisenko et al. 2008
EU096831	ROM117178	Suriname	657	Borisenko et al. 2008
HQ545554	ROM120079	Suriname	657	Lim et al. 2010*
HQ545600	ROM120137	Suriname	657	Lim et al. 2010*
HQ545647	ROM120189	Suriname	657	Lim et al. 2010*
HQ545674	ROM120221	Suriname	657	Lim et al. 2010*
HQ919735	ROM120383	Suriname	657	Lim et al. 2010*
JF447427	ROM104225	Panama	657	Clare et al. 2011
JF447691	ROM117063	Suriname	657	Clare et al. 2011
JF448984	ROM105186	Ecuador	657	Clare et al. 2011
JF448985	ROM105749	Ecuador	657	Clare et al. 2011
JF448986	ROMF40043	Ecuador	647	Clare et al. 2011
JF455174	ROM116713	Guyana	657	Clare et al. 2011
JF455175	ROM119337	Guyana	657	Clare et al. 2011
JF455176	ROM115679	Guyana	657	Clare et al. 2011
JF455177	ROM112628	Guyana	657	Clare et al. 2011
JF455178	ROM111529	Guyana	657	Clare et al. 2011
JF455179	ROM109322	Guyana	657	Clare et al. 2011
JF455180	ROM108937	Guyana	657	Clare et al. 2011
JF455181	ROM108410	Guyana	657	Clare et al. 2011
JF455182	ROM108529	Guyana	657	Clare et al. 2011
JF455183	ROMF39660	Guyana	657	Clare et al. 2011
JF455184	ROM106673	Guyana	657	Clare et al. 2011
JF455185	ROM104828	Guyana	656	Clare et al. 2011
JF455186	ROM98106	Guyana	657	Clare et al. 2011
KU295479	Isolate C1164	French Guiana	579	Thoisy et al. 2016**

(Darriba et al. 2012). Nodal support was evaluated based on 1,000 bootstrap replicates also using GARLI 2.0.

Results

New records. CSJ-m 995: Antioquia Department: municipality of Urrao: Parque Nacional Natural Las Orquídeas: El Macho (06.5414° N, 076.2356° W, 1730 m a.s.l.; Fig. 1: locality 4), collected by J.F. Díaz-Nieto, S. Carvalho-Madrigal, E. Patiño-Castillo, and J.M. Martínez-Cerón, 9 October 2014. **CTUA 753:** Antioquia Department: municipality of Maceo: Hacienda Santa Barbara (06.5441° N, 074.6404° W, 500 m a.s.l.; Fig. 1: locality 3), collected by J. Muñoz, 14 April 2004. **CTUA 1692:** Colombia: Sucre Department: municipality of San Onofre: Reserva Natural Sanguaré (09.7056° N, 075.6815° W, 11 m a.s.l.; Fig. 1: locality 13), collected by D. Gómez, 4 February 2010. **ICN 13747:** Putumayo Department: municipality of Puerto Leguizamo: Parque Nacional Natural La Paya (00.2667° N, 075.0200° W, 230 m a.s.l.; Fig. 1: locality 12), collected by R. Polanco, 15 May 1994. **ICN 14990:** Guainía Department: municipality of Inirida: La Ceiba, Bosque alto (03.6388° N, 067.8826° W, 100 m a.s.l.; Fig. 1: locality 7), collected by A. Cadena, C. Ariza, J. Alvarez, 19 March 1998. **ICN 21030:** Amazonas Department: municipality of Leticia (04.1934° S, 069.9379° W, 84 m a.s.l.; Fig. 1: locality 1), collected by H. Lopez, 29 April 2002.

Comments and Identification. As part of a mammal inventory at the Parque Nacional Natural Las Orquídeas on 9 October 2014, an adult female of *Phylloderma stenops* (Fig. 2) was captured with mist net in secondary forest (northwestern Andean Montane Forest ecoregion) at El Macho, municipality of Urrao, Antioquia Department, Colombia (Fig. 1: locality 4). The specimen CSJ-m 995 is an adult female with an open pubic symphysis, preserved as skin and skeleton, with liver tissue preserved in ethanol (96%), and deposited in the mammal collection of the Museo de Ciencias Naturales de la Salle of Instituto Tecnológico Metropolitano (CSJ-m). It has the following measurements: total length 122 mm; tail length 18 mm; hind foot length 22 mm; ear length 26 mm; forearm length 73 mm; and maximum length of the skull 33 mm.

We confirm the presence of *P. stenops* in 14 localities (19 specimens) for Colombia, 8 of which were previously published and 6 are new (Fig. 1, Table 2). Specimen CSJ-m 995 collected in northwestern Andean montane forests (Fig. 1: locality 4) represents an increase of 830 m in the elevational distribution of the species for the country, and specimen CTUA 1692 corresponds to the first record of the species in the xeric scrubs of northern Caribbean coast (Fig. 1: locality 13), extending the known distribution of the species in Colombia northwared by 534 km. All examined material conforms to the description of the species and the most diagnostic-relevant characters are illustrated in Figures 2 to 5. This is a large species with reported forearm length between 65–81.7 mm and the maximum length of the skull between 29–34.5 mm (Husson 1962, Barquez and Ojeda 1979, Williams and Genoways 2008). It has a face with prominent chin and lip facial projections (excrescences not warts like those found in *Trachops*), noseleaf wide at the base with a pointed tip, short dorsal hairs with reddish-brown color as reported by Salas et al. (2014) (Fig. 2), white wingtips, calcar nearly equal to or shorter than

Table 2. List of records of *Phylloderma stenops* in Colombia. Locality numbers and ecoregions are mapped in Figure 1; asterisk (*) indicates material that was not examined by us (see Methods).

Locality no.	Museum catalog no.	Department	Municipality	Latitude	Longitude	Elev. (m)	Ecoregions	Source
1	ICN 21030	Amazonas	Leticia	-04.1934	-069.9379	84	Solimões-Japurá moist forests	This work
2	TTU 9065*	Amazonas	Leticia	-04.1489	-069.9357	85	Solimões-Japurá moist forests	Marinkelle and Cadena 1972
3	CTUA 753	Antioquia	Maceo	06.5441	-074.6404	500	Magdalena Valley montane forests	This work
4	CSJ-m 995	Antioquia	Urrao	06.5414	-076.2356	1730	Northwest Andean montane forests	This work
5	ICN 14598	Caquetá	Solano	00.0742	-072.4514	130	Caqueta moist forests	Montenegro and Romero-Ruiz 1999
6	UV 4516*	Chocó	San Jose del Palmar	04.9510	-076.2874	900	Northwest Andean montane forests	Alberico 1994
7	ICN 14990	Guainía	Inirida	03.6388	-067.8826	100	Negro-Branco moist forests	This work
8	UV 2747*	Guainía	Inirida	03.2425	-068.1971	100	Negro-Branco moist forests	Alberico 1994
9	IAvH 2217*	Meta	La Macarena	02.5500	-074.0500	283	Caqueta moist forests	Lemke et al. 1982
10	ICN 9612*	Meta	Puerto López	03.9654	-073.0502	190	Llanos	Ramírez-Fráncel et al. 2015
11	ICN 10236*, 10237, 10238*, 10239*, 10240	Meta	San Juan de Arama	03.3461	-073.9306	450	Apure-Villavicencio dry forests	Sánchez-Palomino et al. 1993
12	ICN 13747	Putumayo	Puerto Leguizamo	00.2667	-075.0200	230	Napo moist forests	This work
13	CTUA 1692	Sucre	San Onofre	09.7056	-075.6815	11	Guajira-Barranquilla xeric scrub	This work
14	CZUT-M1330*, 1380	Tolima	Ambalema	04.8488	-074.8138	253	Magdalena Valley dry forests	Ramírez-Fráncel et al. 2015

Figures 2, 3. Pale-faced Bat, *Phylloderma stenops*, adult female (CSJ-m 995). **2.** Individual captured at Parque Nacional Natural Las Orquídeas, Colombia. Photograph by CSG. **3.** Skin of same specimen; scale bar = 25 mm.

the length of the foot, and the tail reaches only half of the inter-femoral membrane (Fig. 3) (Husson 1962, Barquez and Ojeda 1979, Emmons and Feer 1999,Williams and Genoways 2008, Reid 2009, Díaz et al. 2011, Díaz et al. 2016). Although the species seems to be easily identified, specimen ICN 4465 identified by Ramírez-Fráncel et al. (2015) as *P. stenops,* was re-identified by us as *Phyllostomus elongatus* (É. Geoffroy St.-Hilaire, 1810). As previously mentioned, the species is not uncommonly misidentified with members of the genus *Phyllostomus*. Nonetheless, our examined material of *P. stenops* can be easily differentiated from the former genus using dental characters: while *Phylloderma* has 3 lower premolars (the second of which is small and labially oriented) the genus *Phyllostomus* has only 2 premolars similar in size (Figs 4, 5) (Husson 1962, Emmons and Feer 1999, Williams and Genoways 2008).

Our phylogenetic analysis of COI sequences shows 3 salient features (Fig. 6). First, haplotype of specimen CSJ-m 995, identified as *P. stenops* using morphological characters, is nested with other sequences of the species with strong support—and not with any other Phyllostomine genera—implying that the morphological characters are reliable for an accurate identification of this species and delimitation from phyllostomine genera. Second, the Colombian haplotype is sister to the only other available sequence from a trans-Andean locality (Panama), suggesting a trans-Andean clade for the species. Third, cis-Andean haplotypes appear to be paraphyletic and as previously found by other authors (Clare et al. 2011), the material from the Guiana Shield does not form a monophyletic group (Fig. 6).

Discussion

One of our new records, represented by the specimen CSJ-m995, increases the elevational distribution of the species in Colombia by 830 m, as the species had been recorded in the country only up to the 900 m a.s.l. (Alberico 1994); nonetheless, across its distribution (e.g., in Ecuador) this species was known to occur up to 1,750 m a.s.l. (Brito and Arguero 2012), and according to Emmons and Feer (1999) it can reach elevations of 2,600 m a.s.l. Additionally, before our identification of CTUA 1692 from the xeric scrubs in the Caribbean of Colombia (Fig. 1: locality 13), the northernmost known locality of *Phylloderma stenops* for Colombia was from northwestern Andean montane forests, (Fig. 1: locality 6) (Alberico 1994), and consequently our record increases the latitudinal distribution of the species in Colombia by 534 km. Despite our efforts for examining all the available material at the 2 visited collections, we were unable to find several specimens reported by Sánchez-Palomino et al. (1993) and Ramírez-Fráncel et al. (2015). In particular, the single available specimen from the Llanos ecoregion (Fig. 1: locality 10) was not found, and only 2 (out of 5) specimens from the ecotone between montane and dry forests (Fig. 1: locality 11) were found and positively identified as *P. stenops* (Table 2).

Although our phylogenetic analysis using mitochondrial data had only identification purposes, it does show that despite its wide distribution, this species has a reduced mitochondrial variation—only 2.1% within species (*p*-) distance—across haplotypes that cover a wide longitudinal gradient from French Guiana to Panama, and only 0.2% of pairwise (*p*-) distance between the Colombian haplotype and its sister clade of Guyanese sequences (Fig. 6). Although relevant, the issue of the likely paraphyly of Guyanese mitochondrial haplotypes is out of the scope of this paper and should be addressed elsewhere.

Many studies have catalogued *P. stenops* as locally rare but widespread (Handley 1976, Trajano1984, Arita 1993, McDade 1994, Simmons and Voss 1998, Emmons and Feer 1999, Nadkarni and Wheelwright 2000, Reid 2009) and our study seems to provide evidence to reinforcing this concept. As an example, as part of a mammal inventory at Parque Nacional Natural Las Orquídeas, from more than 300 netted bats only a single individual of *P. stenops* was captured (Díaz-Nieto unpublished). Although for Colombia the species is only known for 14 localities, these encompass almost the entire latitudinal and longitudinal gradient of the country as well as a great

Figure 4. Skull and mandible of adult female *Phylloderma stenops* (CSJ-m 995); scale bar = 10 mm.

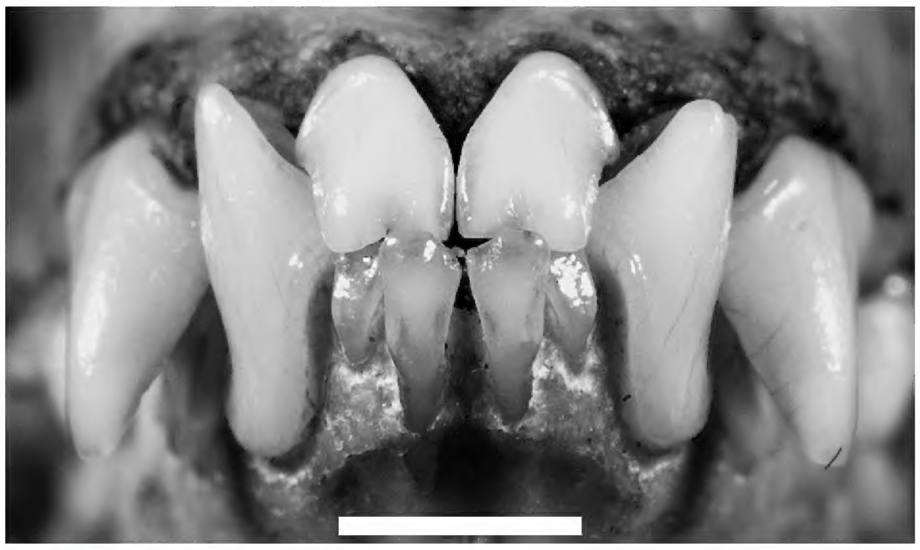

Figure 5. Upper and lower incisors of adult female *Phylloderma stenops* (CSJ-m 995); scale bar = 2 mm.

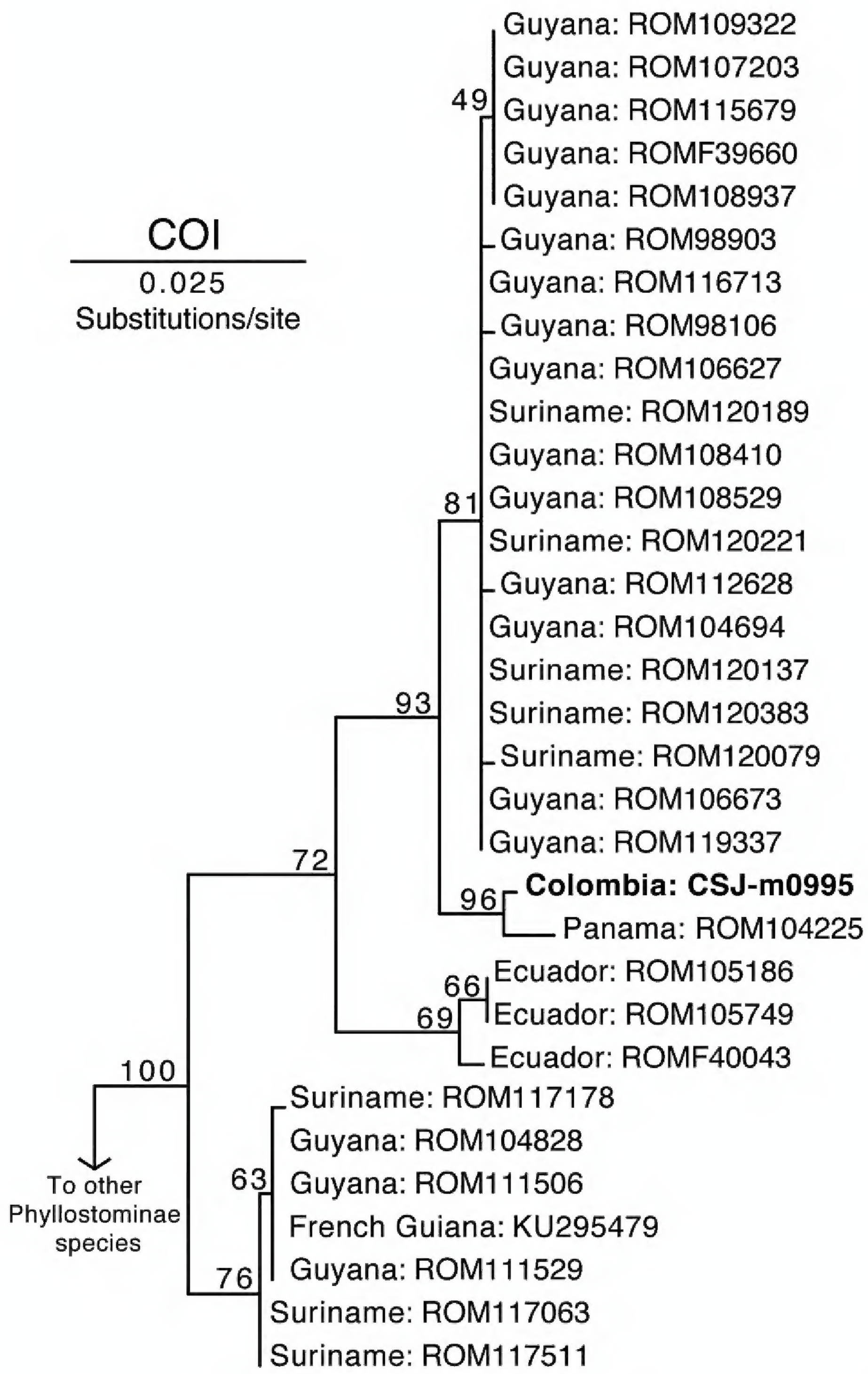

Figure 6. A maximum-likelihood topology of COI sequences of *Phylloderma stenops*. Numbers on branches correspond to bootstrap support values. Each terminal is identified by country of origin and an alphanumeric specimen identifier (see Tables 1, 2). Bolded terminal corresponds to the sequence obtained in this report.

elevational gradient. Such wide geographical distribution includes mostly humid ecoregions (see above) but also at least 2 dry ecoregions, such as dry and xeric shrublands (Fig. 1: localities 11, 13 and 14).

New field-based studies with increased sampling effort should be developed to gain knowledge on the ecogeographic limits of the species, in particular in areas with likely suitable habitat where the species has yet to be found (e.g., biogeographic Choco, Andean montane forests of Cordillera Central and Oriental). Additionally, a denser genetic (multiple loci) and geographic sampling should be useful in testing both the ecogeographic and evolutionary limits of the proposed subspecies, in particular, relevant samples such as those from dry ecoregions and those from the northern and southern limits of its distribution would be welcome.

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Authors' Contributions

JFD, SCM, EPC, and JMC collected the specimen; JMC visited museums to examine material; JMC and JFD analyzed the data; JFD contributed reagents, materials, and analysis tools; JMC and JFD wrote the paper; all authors revised, commented, and edited earlier versions of the manuscript and contributed intellectually.

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